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QUANTIFYING BIRD PREDATION OF ARTHROPODS IN FORESTS

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Abstract. Sampling insects and other arthropods in forest environments is complicated because of the unique attributes of this ecosystem. Entomologists have used many techniques to quantify forest arthropods, some of which are applicable for quantifying the impact of bird predation, as we illustrate in studies of several defoliators and bark beetles. We describe sampling methods for a defoliator, Douglas-fir tussock moth (*Orgyia pseudotsugata*), and a bark beetle, western pine beetle (*Dendroctonus brevicomis*). We discuss the types of information that can be obtained for insect populations from these methods, the time or cost for different levels of sample error, and the application of these methods for evaluating bird predation on arthropods.

Key Words: Sampling; predation; defoliators; insectivorous birds; forests; conifers; western pine beetle; Scolytidae; Douglas-fir tussock moth; Lymantriidae.

Forest entomologists have struggled with the quantification of arthropod abundance for many years. Much work has been done by applied biologists interested in population dynamics of certain species, efficacy of treatments, or the impact of insects on resources. Quantitative studies are more complicated in forests than in other environments where insects are of economic importance (such as agriculture; Dahlsten 1976), because forests are vast, continuous regions composed of different tree species of different ages, and a mosaic of stocking (density) patterns (Pschorn-Walcher 1977). The advantage of forest ecosystems is that they generally encounter less perturbation than agricultural systems and probably have a more stable arthropod community. Outbreak species (those that reach very high densities periodically) are relatively rare in forests (Berryman 1986).

Most studies of forest insect populations deal with single species; associated insects such as natural enemies, inquilines, and organisms in the same feeding guild are often ignored. Regional or forest-type arthropod faunistic or community studies are rare and typically more qualitative than quantitative. Yet, population information gathered by entomologists may be useful in assessing the impact of birds on a single insect species.

Meanwhile, ornithologists desire quantitative population information about arthropod species eaten by birds. Birds typically feed on several different species and at different heights in the foliage. To quantify an adequate number of prey items on several substrates is costly and time-consuming, however, so compromises and stratifications are required.

Based on work by our laboratory, we believe that better quantification of arthropod prey for birds is possible. We have had a long-term interest in the impact of natural enemies on forest insects, particularly insectivorous cavity-nesting birds (Dahlsten and Copper 1979). In this paper we discuss the types of sampling we have used to assess avian impact on insects on two substrates in the forest, foliage and bark, and also what it costs to obtain useful information.

FOLIAGE SAMPLING

LODGEPOLE NEEDLE MINER

The lodgepole needle miner (*Coleotechnites milleri*; Lepidoptera: Gelechiidae), because of its cyclic availability, is a suitable species for studying the role of birds in its dynamics. The adult moths appear only in alternate years and have a short period of activity, whereas the larvae and pupae are available for a long period. The insect has a discrete 2-year life cycle, passing the first winter in an early larval instar and the second winter in the fifth instar. As the birds feed only on larger larvae, this food source is available only in alternate years. In addition, because the insect is a needle miner, the birds must open needles to obtain the larvae, leaving evidence of their feeding. Finally, the distribution of immature needle miners in the trees has been studied and a sampling method developed (Stark 1952, Stevens and Stark 1962). The method is similar to that for tussock moths, discussed below, and involves sampling the tips of lodgepole pine branches.

At a study site in the Inyo National Forest, Telford and Herman (1963) found that Mountain Chickadees (*Parus gambeli*) concentrated their feeding efforts in alternate years on the needle miner larvae and that the chickadees exhibited a functional response to prey density. The chickadees peeled needles in a characteristic way, leaving evidence of their feeding, and Cassin's Finches (*Carpodacus cassinii*) also fed on needle miners by clipping the ends of the needles

(Dahlsten and Herman 1965). Nest boxes were later placed in areas infested and not infested with needle miners. Mountain Chickadees increased in density in the infested areas, both during the breeding and postbreeding periods.

The needle miner-chickadee system has great potential for evaluating the impact of a bird on a single insect species. Because the insect is cryptic during the stage eaten, evidence of chickadee feeding can be easily detected. The system is ideal for studying the functional response of chickadees, because the prey is available only in alternate years, and nest boxes and avian census techniques permit study of the numerical response of the predator to its prey.

Bud-mining Sawflies

Bud-mining sawflies (*Pleroneura* spp.; Hymenoptera: Xyelidae) are also well suited for evaluating avian predation. Four species mine new buds on expanding shoots of white fir (*Abies concolor*) in California; three have been studied in detail (Ohmart and Dahlsten 1977, 1978, 1979). The species of early instar larvae and adults can be distinguished, but the late larval instar (the stage most likely to be eaten by birds) cannot be separated to species.

The three species were treated as a single group in an analysis of within-crown distribution and the development of sampling methods at Blodgett Forest, El Dorado County, California (Ohmart and Dahlsten 1978). Over 94% of the infested buds occurred in the outer portion of the crown, coinciding with the foraging area of several birds at Blodgett, particularly the Mountain and Chestnut-backed (*P. rufescens*) Chickadees. Also, the chickadee nesting period coincided with the late larval instars of the sawflies, late May to early June (Ohmart and Dahlsten 1977).

We did not learn how birds open buds to remove larvae, or if they leave characteristic evidence. However, mortality of the *Pleroneura* fifth larval instar was substantial (Ohmart and Dahlsten 1977), seemingly because of avian predation, as chickadees were observed and photographed by nest box camera units bringing numerous *Pleroneura* larvae to their young.

Pine Sawflies

Larvae that feed in the open, like sawflies, are often fed upon by birds, but no evidence is left on the foliage when they are removed. However, birds often remove sclerotized portions of insects, such as the elytra of beetles and the head capsules of larvae, before eating them or feeding them to nestlings. Sawfly larvae, in particular, exude a brownish substance from their mouth when threatened by a parasitoid or predator. This substance is probably distasteful (Eisner et al. 1974).

In studying the population dynamics of a pine-feeding sawfly in the *Neodiprion fulviceps* complex at Mt. Shasta, California, Dahlsten (1967) watched Evening Grosbeaks (*Coccothraustes vespertinus*) feeding on their larvae. Ten trees, 2–4 m in height, were sampled in each of three study areas at different elevations in a plantation. All sawfly stages, starting with eggs, were counted. Drop cloths were placed beneath each sample tree. The cloths did not catch cocoons, but they did catch head capsules and thoraxes of larvae, which were discarded by grosbeaks. Some larval remains were also stuck to foliage; counts on and beneath the trees showed a total of 166 sawflies—10% of all the larvae on the study trees in one area (Dahlsten 1967).

Because the birds were feeding on a known population, the portion taken was known, at least from the sample trees. Area-wide estimates can be made from such samples. This is a labor-intensive technique, limited to smaller trees where foliage-feeding insects could be counted and larval remains could be found on foliage or drop cloths.

Douglas-fir Tussock Moth (DFTM)

The tussock moth (*Orgyia pseudotsugata*; Lepidoptera: Lymantriidae), because of its economic importance in western North America, has been the focus of many studies, including the role of insectivorous birds in its population dynamics (Brooks et al. 1978; Torgersen et al., this volume). The tussock moth overwinters as eggs in masses on top of female cocoons. Both male and female cocoons are commonly spun on foliage, although cryptic sites such as cavities in trees are also used. The cocoons and egg masses, in particular, are suitable for stocking studies. Egg masses can be sampled and then examined for evidence of predation, or they can be stocked on branches or trunks of trees at different known densities and predation evaluated (Dahlsten and Copper 1979, Torgersen and Mason 1987). Pupal stocking showed that most predation was due to birds, although some was due to ants (Dahlsten and Copper 1979, Torgersen et al. 1983).

Sampling Arthropods on White Fir

This study illustrates how the distribution of a community of organisms on a given tree species can be determined. Sampling programs can then be developed for any species known to be eaten by birds. Relationships among sampling error, time spent sampling, and cost are shown, so that the researcher can better manage available financial resources.

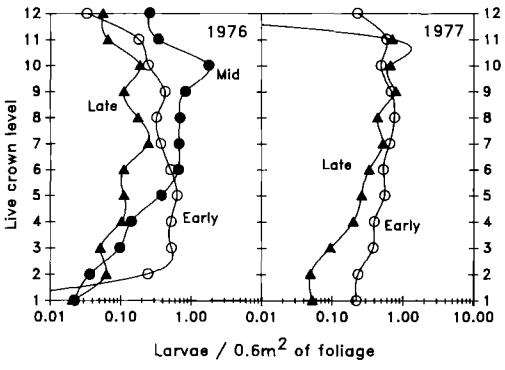

FIGURE 1. Distribution of Douglas-fir tussock moth (*Orgyia pseudotsugata*) on white fir, in 12 equal levels of the crown in different sample periods in 1976 and 1977, El Dorado and Modoc counties, California.

Methods

Two areas in California were selected for sampling, based on Douglas-fir tussock moth activity in previous years. Three plots were established in each area, at Yellowjacket Springs, Tom's Creek, and Roney Flat in Modoc County, and at Iron Mountain, Plummer Ridge, and Baltic Ridge in El Dorado County.

A road ran lengthwise through each plot, which was 2–5 km long. Each plot was divided into quarters; two spots were randomly selected in each quarter. At each spot, the nearest white fir between 9–12 m in height became the first sample tree. Sample spots were permanent and were revisited each subsequent sampling period; since the sampling was destructive, on each subsequent visit the 9–12 m white fir nearest to the originally selected sample tree was chosen.

Eight trees, one from each of the eight spots in a plot, were sampled in each of the six plots during each sample period, giving a sample size of 48 trees per period. Five periods during the DFTM generation were sampled in 1976: Period 1 = late spring–early summer for cocoons and egg masses laid by the previous generation; Period 2 = early larval stage; Period 3 = midlarval stage; Period 4 = late larval stage; and Period 5 = a final sample in early to late fall for the cocoon-egg mass stages. The five trees in each spot therefore spanned the development of the DFTM generation and gave phenological information for the DFTM defoliator guild, and for its predators and parasites.

For each sample tree, all live branches were numbered beginning from the lowest north-side branch. Computer-generated random number lists were used to select a sample of one-third of all branches on the tree. All branches were cut from the tree; branches selected for sampling were caught in large canvas bags and beaten over a large canvas on the ground. All insects and spiders were recorded, as was the branch number, dimensions (for foliage area), and other characteristics. Some insects were retained for rearing or identification. A crew of three or four, processing from two to four trees per day, was needed for the intensive sampling procedure.

During periods 1 and 5 (spring and fall) sampling was supplemented by a 100% search for DFTM cocoons and egg masses, as these occur in relatively low numbers. These data were kept apart from the regular sample.

In the second year of sampling (1977), some modifications were made. Because cocoons and egg masses were rare in 1976, only the two plots with the most cocoons and egg masses in 1976 were sampled during the first and fifth periods of 1977, and no sampling was done during period 3 (medium larval stage).

Field data sheets were designed for direct keyboard entry, and computer programs were written to produce summaries of each insect species' density by whole trees, plots, areas, and by each of 12 equal crown levels. Another program was written to simulate sampling in different ways, such as two midcrown branch samples, two branches at each of three crown levels, and so on. This program gave variance, bias, and cost figures necessary to sample a plot at any level of precision for each sampling method.

Results

Foliage distributions of DFTM, *Neodiprion, Melanolophia* sp., and associated insects were calculated by 12ths of the live crown from the whole-tree sample of 48 trees per period, with both areas combined. Numbers of egg masses and cocoons in periods 1 and 5 were too low to estimate meaningful distributions. Many empty cocoons were found, presumably a result of avian predation.

Distributions of small, medium, and large larval DFTM differed by crown level and by years (Fig. 1). Early summer (small larvae) distribution was relatively constant across levels in 1976 except for the lower and upper foliage, whereas in 1977 density increased steadily from the lower to the upper one-fourth of the foliage. Late summer (large larvae) distributions tended to increase by a factor of 10 or more from the lower one-third to upper one-third of the trees, with the 1977 trees showing considerably higher density in the upper crown. The unpredictable changes indicate the need for multilevel crown sampling to avoid biased estimates.

Live crown densities of *Neodiprion* larvae for late spring were very low ($<0.2/0.6$ m^2) in 1976 and almost zero in 1977 (Fig. 2). In early sum-

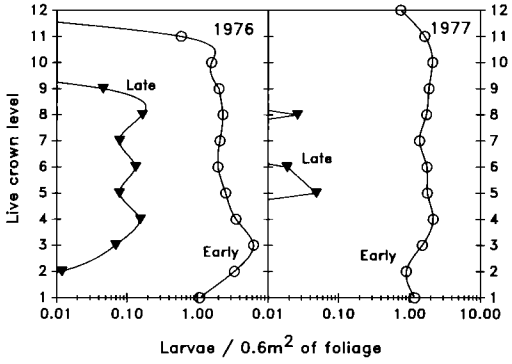

FIGURE 2. Distribution of sawfly larvae (*Neodiprion* species) on white fir in 12 equal levels of the crown in different sample periods in 1976 and 1977, El Dorado and Modoc counties, California.

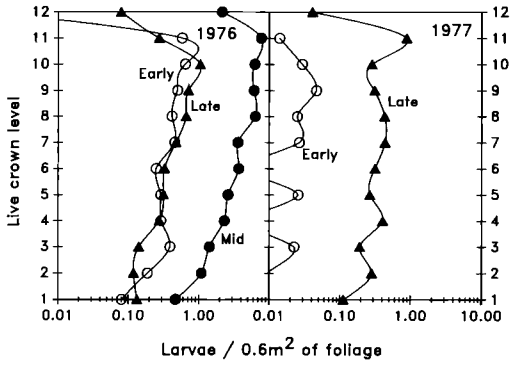

FIGURE 3. Distribution of greenstriped forest looper larvae (*Melanolophia imitata*) on white fir in 12 equal levels of the crown in different sample periods in 1976 and 1977, El Dorado and Modoc counties, California.

mer, the density jumped to high levels, especially in 1976 (peak of >6/0.6 m²). The distributions of early summer populations varied markedly between the two years, with higher densities in the lower one-third crown in 1976, but relatively even distributions across levels in 1977 (Fig. 2). Sampling for this insect would require a multilevel technique to reduce bias to an acceptable level. A sample of the lower one-third crown level would estimate that the 1976 density was 3–4 times higher than in 1977, whereas the whole-tree density of the intensively sampled trees indicated 1976 was only about 1.5 times higher. This insect also illustrates the timing problem in estimating prey density; its density increased about 20 times between late spring and early summer and then dropped to near zero by mid- to late-summer (not shown).

Another known chickadee prey, the greenstriped forest looper, *Melanolophia imitata,* a common geometrid larva on white fir, did not appear in significant numbers until early summer in 1976 and 1977. Densities rose from about 0.5/0.6 m² in early summer to about 5.0/0.6 m² in midsummer, and then dropped to about 0.5/0.6 m² by late summer of 1976 (Fig. 3). Distributions were biased toward the upper third of the live crown during all periods. In 1977, density in early summer was about ten times lower than in 1976, but in late summer was similar to 1976 (no midsummer sample was taken). Possibly a single level sample, probably at midcrown, could be used with minimal bias, if the low/middle/upper ratios seen in these two years were consistent over a number of years.

If the objective of sampling is to estimate total prey availability in foliage, a multilevel sample will be required for relatively precise, unbiased estimates. To illustrate this, we used computer-generated sub-sampling of the original data from all trees, under a variety of sampling rules, to compare their DFTM density estimates to those using the complete intensive sample. We then used estimated cost figures to determine the most efficient methods for given total error levels.

The computer sampling program simulated these sampling methods: two branches taken at random from the lowest two meters (lower two meter sampling method); two branches from the middle ⅓ of the crown (midcrown sampling method); two, three, or four branches from the whole crown at random (whole crown–two branch method, whole crown–three branch method, etc.); two, three, and four equal crown levels, with sets of two, three, or four branches from each level (giving nine methods, for example the two level–two branch per level method, three level–three branch per level method, and four level–four branch per level method). For each of these methods the program calculated tree mean densities using means per level weighted by the average proportion of foliage per level.

Within-tree sampling error (WSE) was the square root of the variance of the density estimates for all possible samples. Between-tree errors (BSE) were calculated from the mean squared differences between area means and individual tree means. Bias was found by subtracting the density mean (SM) of the samples chosen by the program from the "actual" (intensive sample) tree mean density (AM). Total standard error (TSE) for a sampling method with n sample trees was then calculated as:

$$TSE = \sqrt{((BSE^2 + WSE^2)/n + BIAS^2)}$$

where BIAS = AM − SM.

It is important to use a sampling method with low and stable bias, because bias cannot be re-

TABLE 1. DOUGLAS-FIR TUSSOCK MOTH SAMPLING SIMULATION: PERCENT MEAN BIAS[a] OF DIFFERENT SAMPLING METHODS FOR DOUGLAS-FIR TUSSOCK MOTH FOR PERIOD 2 (SMALL LARVAE), 1976 AND 1977

Number of branches per division	Year	Divisions					
		Lower 2 m only	Mid-crown only	Whole crown	2 Level	3 Level	4 Level
2	1976	−94.3	58.1	4.9	0.9	1.4	3.1
2	1977	−85.3	59.5	10.3	8.7	6.1	11.6
3	1976			3.0	2.3	2.3	4.0
3	1977			6.6	7.7	5.1	10.5
4	1976			2.0	2.9	2.7	4.4
4	1977			4.7	7.2	4.7	10.0

[a] Percentages of unbiased means of 0.333/0.6 m² (1976) and 0.434/0.6 m² (1977).

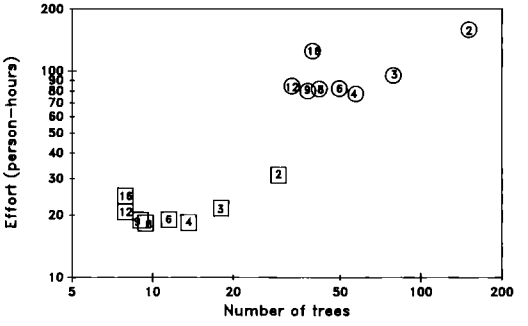

FIGURE 4. Effort to sample Douglas-fir tussock moth (*Orgyia pseudotsugata*) on different numbers of trees with varying numbers of branches per tree (numbers are the number of branches from 2–16) with 20% standard error (circles) and 40% standard error (squares). Based on 1977 period 2 small larvae sampling, El Dorado and Modoc counties, California.

duced by increasing sample size. The methods tried above using two, three, or four branches from two or three levels generally yielded the lowest percent bias figures (Table 1 shows DFTM small larvae for two years). The percent bias for both the lower two meter method and the mid-crown method was high and unstable.

Comparisons between methods may be made by selecting an acceptable level for TSE and calculating the number of trees and total branches required for a given mean density and its associated BSE, WSE, and BIAS. Labor costs may then be calculated from the estimated time to locate a tree and sample a branch. A conservative estimate is 15 min per tree, plus three min per branch for a crew of three people.

For example, in 1977 the mean density of small larvae (Period 2) was 0.434/0.6 m², the WSE varied from 0.181 to 0.804, and the BSE varied from 0.409 to 0.441, depending on the sampling method. Total trees and effort needed to determine the mean with a TSE of 20%, 40%, or 60% of the mean were calculated for each method, and trees were plotted vs. effort for different methods at two error levels (Fig. 4). Only the low bias methods and more efficient of any two methods that used the same number of branches per tree are shown.

For any error rate, the minimum point for curves in terms of effort indicates the most efficient sampling for the time assumptions used. The three-level, two-branch-per-level method is a good choice, as it is easy for field crews to divide a crown by eye into three levels, and it ensures a relatively representative sample, even if the branches chosen in each level are not random. Methods using greater numbers of branches are more likely to cause significant damage to the tree.

Tree and effort figures were calculated for all the sample periods in both years. Relationships between methods for other periods were similar to those for Period 2, 1977. However, the numbers of trees necessary for a given proportional sample error increased significantly for sample periods with lower mean densities. Using the three-level, two-branch-per-level method, the number of trees necessary for standard errors of 20%, 40%, and 60% of the mean was calculated and plotted vs. density, along with least squares regression lines for each error level (Fig. 5). This figure can be used to plan a low-level population sampling program, given the degree of precision required and an estimate of the populations in an area, perhaps from the previous year's population or a pilot study. Such methods are costly, but they can provide estimates of prey species abundance with reliable error rates and low bias.

BARK SAMPLING

Sampling of the bark substrate by our laboratory has mostly been below the surface of straight-boled conifers for species such as bark beetles (Scolytidae) and scales (Margarodidae). This group of cryptic, bark-inhabiting arthropods has special advantages for evaluating avian predation. One is that bark foragers and gleaners can be excluded by screening. Another is that birds usually leave evidence of feeding on insects in the phloem-cambial region, such as flaked or holed bark. However, sampling is often labor-intensive and costly. Below are examples of specific attempts to evaluate avian predation and of costs of sampling programs.

WESTERN PINE BEETLE (WPB)

The biology and control of the western pine beetle (*Dendroctonus brevicomis*; Coleoptera: Scolytidae) has been a problem for over 80 years

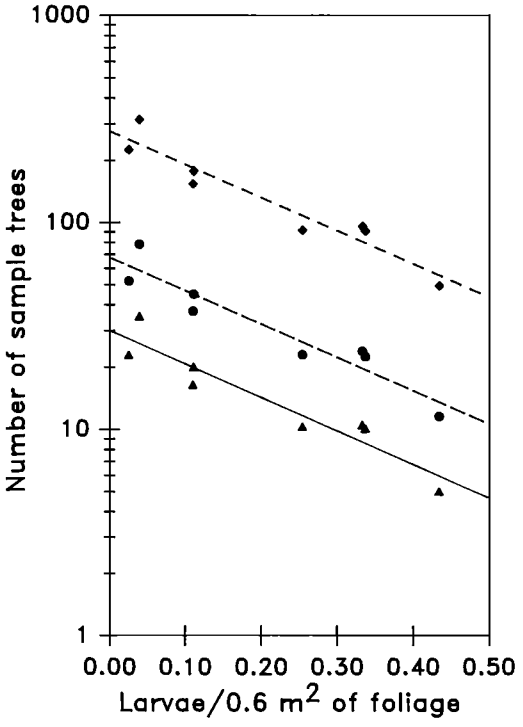

FIGURE 5. Number of sample trees needed for sampling Douglas-fir tussock moth (*Orgyia pseudotsugata*) at different densities for standard errors = 20% of mean (diamonds), 40% of mean (circles), and 60% of mean (squares), using the three-crown-level, two-branch-per-level method.

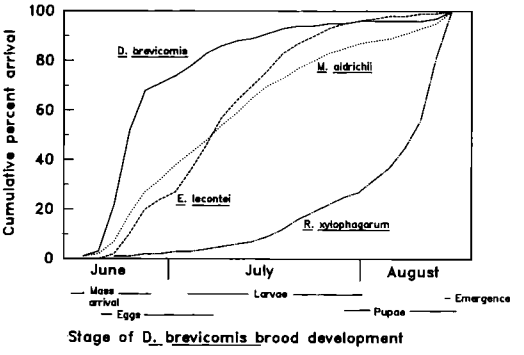

FIGURE 6. First generation arrival patterns of western pine beetle (*Dendroctonus brevicomis*) (8334 individuals) and three representative species of associates totalling: 3480 *E. lecontei*, 1684 *M aldrichii*, and 2728 *R. xylophagorum*. Data are mean cumulative frequencies from five trees at Blodgett Forest in 1970 and 1971. The mean collection interval was 2.5 (±0.06) days, and the mean trapping period was 62.8 (±1.6) days. The approximate stages of pine beetle within-tree brood development are shown (from Stephen and Dahlsten 1976b).

(Miller and Keen 1960, Stark and Dahlsten 1970). Their attack and colonization of ponderosa pine (*Pinus ponderosa*) has three phases (Wood 1972): (1) dispersal from the overwintering generation and selection of new susceptible trees in early spring (May and June); (2) concentration (mass attack) by feeding females; and (3) establishment that is associated with mating, excavation of egg galleries, and brood development. This same sequence occurs for a second generation that is usually prolonged, and which may overwinter as late larvae or pupae. However, in warm years a third generation may develop in October–November. In each generation, starting with the mass-attack phase and throughout the establishment phase, numerous other arthropods, parasites, and predators are attracted to the developing brood in a sequential pattern (Fig. 6).

In order to obtain information on the arrival pattern of pine beetles (Stephen and Dahlsten 1976a) and the subsequent arrival of associated arthropods, it is necessary to find trees just as they are under mass attack (Stephen and Dahlsten 1976b). Because locating sample trees was difficult, we induced mass attack by using female-infested bolts (logs) hung in trees (about 6 m from the ground), or by using synthetic attractants hung in trees.

We trapped insects continuously at the bark surface at three heights (1.5 m, 4.5 m, and 7.5 m) of the bole. A pulley system was installed so that a series of Stickem® coated traps could be removed and replaced easily. Traps were changed every other day during the concentration and establishment phases, and every fourth day during brood development. Traps were cleaned in warm kerosene to dissolve the Stickem®. Insects were separated from the solution by fine mesh screens and placed in alcohol.

Estimates of attack densities, gallery length, eggs laid, and brood development were recorded for correlation with arrival patterns of associated arthropods. Since the western pine beetle develops within the bark, an X-ray technique was used to count larvae, pupae and adults, along with some predators, parasitoids, and associates. Also, predation by woodpeckers was estimated visually; see Berryman and Stark (1962), Stark and Dahlsten (1970), and Dudley (1971) for details.

We found that initial beetle attack occurs at midbole, then spreads down and more slowly upward (cf. Miller and Keen 1960, Demars 1970). Height appears to influence brood distribution within trees more than aspect. Also, differences in trapping densities and generations (season) indicate a faster developmental time during the first generation and a higher concentration of

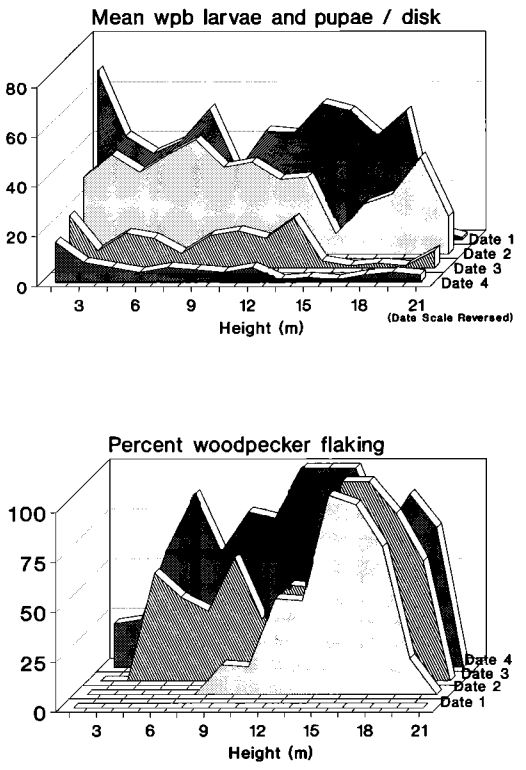

FIGURE 7. Changes in western pine beetle (wpb) (*Dendroctonus brevicomis*) larvae and pupae (UPPER) and percent bark flaking by woodpeckers (LOWER) by height and sample dates (1 = 16 Sept., 2 = 4 Oct., 3 = 10 Nov., 4 = 16 May, date scale reversed for visibility, UPPER only). Three trees combined, Blodgett Forest, California, 1967–1968.

broods in the lower portion of the bole in the second generation.

Western Pine Beetle and Woodpeckers

Because the bark beetle larvae develop within the bark during the later life stages, radiographs (X-rays) of bark samples made larvae easy to count; in many cases predators and parasitoids could also be counted (Berryman and Stark 1962, Berryman 1964). Otvos (1965, 1970) used this technique to determine the combined effect of the four main species of woodpeckers by comparing samples from caged and uncaged portions of trees and by examining bark samples (Stark and Dahlsten 1970). Otvos (1965) first examined all beetle-killed trees (438, from years 1961–1963) in the study area to determine generation and species of beetles killing the trees. He also determined that 53% of the trees had been drilled by woodpeckers, with the most activity occurring on the overwintering (second generation) broods. Otvos' radiograph data (1962–1964 generations) showed 31.8% brood consumption by woodpeckers. A more significant benefit of woodpecker activity was increased parasitism. Otvos estimated that a 3–10 fold increase in parasitism may result from reduction in bark thickness by providing parasites with shorter ovipositors a larger area of oviposition.

Otvos (1970) also measured the western pine beetle broods removed by woodpeckers by X-raying bark strips and plotting positions occupied within the bark by larvae. Among 379 larvae, 220 (58%) were located within the woodpecker-flaked portion of the bark. Additional larval mortality in the thinner bark could also be caused by desiccation and by freezing during the winter months.

A similar study of an overwintering generation of bark beetles in 1967 (Dahlsten, unpubl. data), corroborates Otvos' (1965) results. In this case, bark thickness and percent of woodpecker activity were taken directly from bark samples of infested trees.

We removed pairs of 88 cm^2 bark disks on opposite sides of the bole at 1.5 m intervals from the base to the top of WPB infestation. The first sample date was shortly after the peak of attacks and adult gallery construction, and subsequent samples were spaced through larval stages to the emergence of brood adults. Each sample was X-rayed so that insects within could be identified and counted quickly without dissection of the sample, and the proportional area of bark surface flaked by woodpeckers was recorded.

We found the lowest density of WPBs per disk later in the sampling season when the percent of bark with woodpecker flaking was highest (Fig. 7). Data were from a single generation (1967 overwintering) and represented the mean at each height for three trees close together at Blodgett Forest, California. This pattern is common in the overwintering bark beetle populations. The initial bark beetle attacks probably took place between 7.5 and 12.0 m and fill-in attacks occurred between 1.5 and 18 m. By the second sampling date, woodpeckers had become active high in the tree and the beetle brood showed the reduction at that level. Woodpecker activity continued down the bole on the next two sampling dates, and the beetle brood declined further.

Decline of the beetle brood (in this case brood is the offspring of all females attacking the tree) was not entirely due to woodpeckers. Predatory insects were present prior to woodpecker activity and began to increase at heights below peak woodpecker activity (Fig. 8). (Woodpeckers no doubt feed on predaceous insects also.) WPB larvae infected with parasites attained their highest densities in the upper portion of the tree during

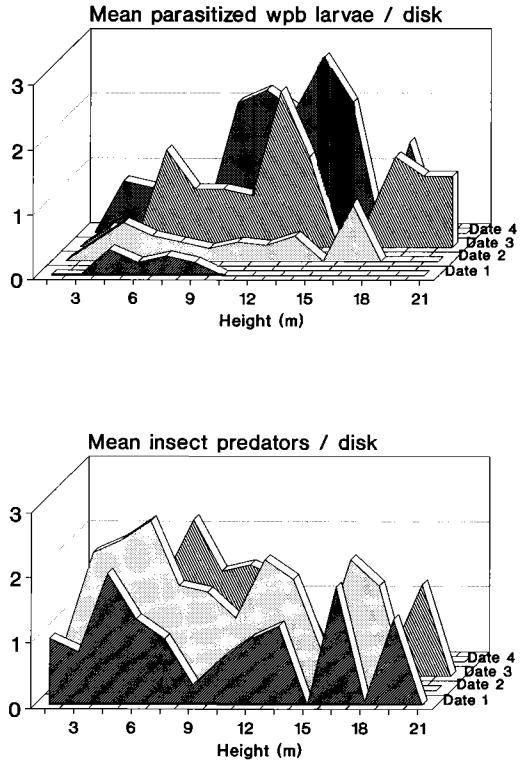

FIGURE 8. Changes in numbers of parasitized western pine beetle (wpb) (*Dendroctonus brevicomis*) larvae (UPPER) and insect predators (LOWER) by height and sample dates (1 = 16 Sept., 2 = 4 Oct., 3 = 10 Nov., 4 = 16 May). Three trees combined, Blodgett Forest, California, 1967–1968.

TABLE 2. ESTIMATED TIME AND COSTS FOR SAMPLING WESTERN PINE BEETLE WITHIN TREE DEVELOPMENT STAGES AND ASSOCIATED ARTHROPODS AND WOODPECKER ACTIVITY. ASSUMPTIONS ARE: TWO TRAINED PERSONNEL, FOUR SAMPLE HEIGHTS PER TREE, TWO SAMPLE DISKS CUT PER HEIGHT PER SAMPLE DATE, AND TWO SAMPLE DATES

	Person-hours
Field sampling	
Locate sample tree (highly variable)	
First sample date (includes setup, limbing,	2.0
installing ladders, and so on)	6.0
Second sample date (includes removal of emergence cartons, measurement for woodpecker bark flaking)	4.0
Field total:	12.0
Lab analysis	
First sample date (eight sample disks)	
Count attacks, eggs, gallery length	4.0
X-ray samples, measure bark thickness	0.5
Read X-rays twice	2.0
Place disks in rearing cartons, periodically check over 6-week period	3.0
Second date (eight sample disks, eight emergence cartons)	
X-ray samples, measure bark thickness	0.5
Read X-rays twice	2.0
Place disks in rearing cartons, periodically check over 6-week period	3.0
Emergence cartons: count known arthropods	2.5
Lab total	17.5
Grand total per tree	29.5

the last sample date. Parasitization was also shown to be enhanced by woodpecker activity in an earlier Blodgett study (Otvos 1965).

To evaluate woodpecker-prey relationships in this system, at least two sample dates are required per WPB generation—one shortly after the peak of the WPB egg stage and prior to woodpecker activity to measure initial larval and egg densities, and another near the emergence stage for brood adults (Table 2). Because woodpecker activity and larval density vary by location, sampling to be representative must include at least four heights along the infested bole. The X-ray technique is probably the fastest method to determine bark beetle numbers within the bark, but it requires some special equipment and training. The cost for this type of sampling is shown in Table 2 on a per tree basis.

MOUNTAIN PINE BEETLE

Larvae of mountain pine beetles (*Dendroctonus ponderosae*; Coleoptera, Scolytidae), unlike those of western pine beetles, develop at the bark–wood interface, not in the bark. The mountain pine beetle has been recorded from many host species (McCambridge and Trostle 1972), and the parasite-predator complex differs by host and location. Dahlsten and Stephen (1974) began to record the associated fauna of mountain pine beetles from sugar pine (*P. lambertiana*) in California. One tree had numerous woodpecker strikes that could be associated with a larval or pupal chamber when the bark was peeled back; 436 individual woodpecker strikes were recorded from the sample bolts, 70% in the upper half of the tree. Because the mountain pine beetle pupae and larvae are beneath the bark, woodpeckers make individual strikes. Cost estimates for different sample sizes were developed for sampling mountain pine beetles in another study (Table 3).

CONCLUSIONS

We have shown that sampling forest arthropod populations is difficult. It can be labor intensive, time consuming, and expensive; moreover, results may or may not help determine the impact

TABLE 3. ESTIMATED TIME NEEDED TO SAMPLE MOUNTAIN PINE BEETLE POPULATIONS[a]

Sample	Hours to remove bark samples	Hours to analyze samples
1000-cm² rectangle, six/tree	1.50	0.90
500-cm² rectangle, six/tree	1.00	0.60
250-cm² rectangle, six/tree	0.70	0.40
100-cm² circular disk, six/tree	0.25	0.25

[a] Cost of locating, felling, and measuring tree and infestation parameters about $80.00.

of avian predators upon their prey. Estimates of arthropod populations can be made, but a proportion of arthropod prey will not be found by any sampling technique.

A decision must be made whether to examine the impact of one bird species or the entire forest bird community upon one or several forest arthropods. It may be easier to obtain more accurate quantitative results when working with only one insect species; yet, all lifestages must be included. A continuous annual study should be attempted to produce good results from this type of investigation.

Another approach may be to intensively sample an entire forest arthropod community occupying a single species of tree. Arthropod samples could then be compared with arthropods found in a bird's diet, which can usually be determined from feces or stomach samples, by visual observation, and in photographs from cameras attached to nestboxes. Correlations could then be made between arthropods within a bird's diet, location of the same arthropod species on a sampled tree, and the locations where the bird spends most of its time foraging on the tree. Avian impacts on arthropod prey could then be assessed by plotting the percent of time birds forage vs. the abundance of specific arthropods at foraging locations.

In general, sampling a limited prey resource quantitatively is the most feasible method for measuring the impact of a predator upon its prey.

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